

JOURNAL
OF THE
BOMBAY NATURAL
HISTORY SOCIETY

1960 APRIL

Vol. 57

No. 1

Studies on the Reproductive Behaviour
of the Baya Weaver [*Ploceus
philippinus* (L.)]

BY

JOHN HURRELL CROOK

Ornithological Field Station, Madingley, Cambridge

(With one plate, one text-figure, and three diagrammatic schemes)

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I. INTRODUCTION

The present paper is a continuation of studies on the biology of the Indian weavers initiated by Dr. Sálim Ali in 1930 and resumed in 1953 (Ali & Ambedkar 1956, 1957, Ambedkar 1958, in preparation). It is also part of a programme of research on the ethology and social organisation of the Ploceinae started at the Ornithological Field Station of the Department of Zoology, Madingley, Cambridge, in 1954. Observational methods used in West Africa in 1955 and 1956 have been employed in India so that accounts of the behaviour of species in both the Ethiopian and Oriental regions may be directly and precisely compared (See Crook 1958, 1959, 1960, in press : *a*, *b*).

The Baya Weaver (*Ploceus philippinus*) is a polygamous species whose life history and general behaviour have been well described (Ali 1930, Ali and Ambedkar loc. cit.). In the Bombay and Poona areas it breeds in the monsoon season siting its nest colonies typically either in tall palms, usually over water, or in vegetation hanging over deep wells. Occasionally small colonies may be found in trees without protection from water but such sites are decidedly infrequent. The male establishes and defends one or two nests, constructing them as far as the 'helmet stage'¹ (Ali 1930, Crook 1960) at which they are maintained until, following a courtship involving much 'nest advertisement display' and mutual antagonism, they are accepted by females. The male may have up to three wives whom he acquires successively in a very short period.² Details of clutch size, hatching success, mortality, growth rate of young, and fledgeling success have been studied in part (Ali & Ambedkar loc. cit., Ambedkar 1958) and the work remains in progress.

In this paper certain new observations made during the 1958 and 1959 seasons are described and, in particular, a detailed account is given of the territorial and sexual behaviour of the species together with a brief analysis of the data.

1. Methods

Detailed observations from hides, through 8×30 binoculars and a ×20 telescope, were made at several wild nesting colonies around Poona, particularly those at Hingane, Parbati Hill, and near the Agricultural College. The changes in behaviour of the weavers are most rapid and in

¹ The terms referring to stages in nest construction have been used in previous publications (Ali 1930, Ali and Ambedkar loc. cit., and Crook in press *a*). They are (i) Wad—the first bunch of strands woven into a nest site, (ii) the Initial Ring—the ring that develops from the wad, (iii) the Helmet Stage Nest—the roof flange projects both before and behind the initial ring from above, (iv) the Completed Egg Chamber—egg chamber complete but no tube, (v) complete nest and lengthening tube present.

² V. C. Ambedkar reports a single case of 5 females to a male in 1959 at Poona.

order to obtain a high degree of accuracy an EMI field tape recorder was used in making commentaries on the sequences of behaviour observed. Such commentaries provide the basis for the quantitative data found in the Schemes¹ and described in the text. The recorder was also used in taping the song and cries of the species which will be later analysed by sound spectrograph at Cambridge and used in a comparative study of the vocalisation of the sub-family. A number of simple experiments were made in which nest positions etc. were modified in order that certain aspects of territorial behaviour might be revealed. The results of a programme of nest mutilation experiments will be published separately.

2. The colony sites

The types of site chosen by the birds for their breeding colonies are shown in Table I. Of 35 colonies 29 (i.e. 82.8%) were situated over water and of these 23 (i.e. 65.7% of the total) were hanging either within wells or in trees over them. Only 6 active colonies and occasionally small groups of adults and colonies of juveniles with unoccupied nests were found away from water. In Kumaon several colonies in bhabar country were also located in small thorny bushes without water near them but in the terai most colonies were again hanging over pools or streams.

A fair amount of polemic has centred around the survival value of the siting of weaver colonies over water. Very similar sites are used by certain colonial species in Africa. Lack (1954) supports the argument that 'colonial nesting is possible only for species which are comparatively safe from nest predators, which otherwise would be attracted to the spot'. The sites of avian breeding colonies are normally protective, at least against crippling predation, and the case of cliff-dwelling sea birds is particularly to point here. In the colonial weavers the chosen sites normally appear to be protective either through association with tribal villages (e.g. *Ploceus cucullatus* in West Africa), through breeding in dense thorny bushes, e.g. the *Quelea* in Senegal, (Crook in press *a*), or through siting over water. Actual observations of predators failing to obtain their prey as a result of these factors are relatively few (Crook 1958, 1960); but the fact that there are such accounts does indicate that predators do attempt to enter the nests and that they do fail. The main dangers to a Baya colony are crows (*Corvus splendens*, Ali 1956, and also almost certainly *Corvus macrorhynchos* in the Poona area) which bore holes in the nests and feed on eggs and young, and also the nocturnal tree mouse, *Vendeluria oleracea*, which may destroy a brood and establish its nest within that of the Bayas (Ali & Ambedkar 1956). However, this species also builds nests and has young in old nests prior to the reoccupation of the colony in spring so that its breeding is not dependent upon a fresh nest. Against these dangers the Bayas have little protection,

¹ For Schemes see pp. 42-44 below.

though the crows' entry to the colony occasions great excitement and mild mobbing. The Striped Squirrel (*Funambulus palmarum* and *F. pennanti*), certainly a potential predator of eggs, which inhabits the vegetation of wells never climbs out on the dangerously fine twigs from which the Bayas suspend their nests. V. C. Ambedkar (personal communication) has a magnificent account of a snake which was observed on a Baya's nest

TABLE I

Sites of breeding colonies of *Ploceus philippinus* in the Poona area 1958 and 1959.

Site	No. of colonies observed	Percentage of total number of colonies
Tall palms over water	2	5.70
Trees overhanging streams	3	8.55
Tree projecting from cliff over stream	1	2.85
Trees over wells	5	14.28
Vegetation hanging within wells	18	51.42
Trees on steep bank away from water	1	2.85
Trees/bushes not near water	3	8.55
Small tree in garden near house	2	5.70
TOTAL	35	..

hanging over the water and attempting to find an entrance. The snake seemed to find difficulty in gripping the nest which contracted under pressure. It edged its way down and tried to get in the tube. However, at this point, it slipped and fell into the well. This provides good evidence not only for the protective value of the siting but also of the nest form itself.

The Bayas are also extremely particular about the siting of the actual nest. Fine down-hanging twigs are normally used and the resulting nest is well separated from near-by prominences upon which predators might perch while opening it. Further, all projections, such as leaves and leaf bases on the supporting twig, are meticulously plucked off leaving the whole support and the nest surface as bare as possible. This could be a factor preventing predators, such as snakes, getting a grip on the support or alternatively it may reduce the surface area thus lessening sway in

winds. This latter point is, however, hardly relevant to nests within the shelter of wells.

It thus appears that both the siting of whole colonies and of individual nests are usually appreciably protective against potential predators. Nevertheless the fact that 17.1% of all the colonies found did not appear to be in a protective site is of obvious significance. Most of these cases were found in the upland area near Karakwasla away from the river valleys and where there are no wells or deep surface streams. It appears then that, where protective sites are not available, the weavers can and do breed without them. It is not known what effect this has on survival. One may suppose that the type of site most common in any one area represents a 'tradition' of site selection in the Baya population brought about by the selection of the most successful (i.e. most protective) sites in the course of many generations.

3. Polygamy and numbers of nests per territory

The male Baya normally pairs with several females whom he establishes successively in the helmet stage nests prepared for their inspection. Assuming that the ratio of males to their nests in the colonies is taken from a representative sample of all adult birds, Ali & Ambedkar (1956, 1957) have concluded that the tertiary sex ratio is therefore 1 male : 2 to 3 females. This ratio excludes the large population of males in their first year which neither attain adult plumage nor breed successfully till their second year. Females of the first year mate and breed successfully.

During Phases II and III of the breeding season in 1958 (see p. 21) the numbers of females paired to a male were studied in relation to the number of nests the male had built and was maintaining in a fresh condition at the time. The results are given in Tables II and III. The majority of males were mated to a single female (53.6% of total territories examined), a fair number (34.1%) to two females, and very few birds (7.3%) to three females. Further, two territories were noted in Phase III in which the males still hopefully maintained helmet stage nests which no females had occupied. In no case did a male complete a nest that was not occupied by a female. In 78% cases a helmet stage nest was maintained in addition to completed nests. The mean number of both completed nests and females per territory was 1.13 (15 territories and 17 females) at Hingane, 1.5 (16 territories and 24 females) at the Parbati Hill area, and 1.8 (10 territories and 18 females) at the Agricultural College. The mean for all the territories examined is 1.44, thus giving a lower tertiary sex ratio in the breeding colonies than previously supposed. The numbers of structures maintained by males in their territories irrespective of their stage of construction are given in Table IV.

TABLE II

Number of females per territory in three different colony groups in the Poona area. (Total number of territories examined : 41)

	Hingane colony (Tree over well)	Parbati Hill colonies (Bushes over wells)	Agricultural College colony (Palm tree)	Totals of territories
Territories unoccupied by females	2	2
Territories occupied by 1 female	9	10	3	22
Territories occupied by 2 females	4	4	6	14
Territories occupied by 3 females	..	2	1	3
Mean number of females per territory	1.13	1.5	1.8	1.44

TABLE III

The construction stages of nests maintained by males in territories occupied by 1, 2, or 3 females respectively. (Number of territories examined : 41. The numerals represent the number of territories of each nest composition.)

Territories of differing nest composition occupied by 1, 2, or 3 females	Hingane colony	Parbati Hill colonies	Agricultural College colony	Total of territories in each category
Unoccupied territories : 1 Helmet stage nest only	2	2
Territories occupied by a single female :				
1 Helmet stage plus 1 complete nest	8	10	1	19
0 Helmet stage, 1 complete	1	1
2 Helmet stages plus 1 complete nest	1	..	1	2
Territories occupied by two females :				
1 Helmet stage plus 2 complete nests	3	3	3	9
2 Helmet stages plus 2 complete nests	1	1	3	5
Territories occupied by three females :				
0 Helmet stage nests, but three complete ones	1	1
1 Helmet stage nest plus three complete ones	..	2	..	2

TABLE IV

The number of structures maintained by males in their territories irrespective of their stages of construction. (Phases II and III of breeding)

Number of structures in territory	Number of cases
1	3
2	24
3	12
4	2

From the above discussion we may note the following points :

- i. While the actual tertiary sex ratio in the three colony areas studied was only 1 male : 1.44 females, the males nevertheless normally maintained an additional structure at the helmet stage ready for any female that might accept it.
- ii. The numbers of females and completed nests per territory appear to differ in the three areas studied (Table II). In particular the colony high in a palm tree had a greater mean number of females per territory than those established over wells. A contingency test shows χ^2 to be 9.23 for which p lies between .1 and .2. Although the differences are not thereby shown to be significant this could be due to the numbers available for the test being small. It is thus possible that a real difference does exist. Such a difference could be due to the greater density of potential nest sites on the palm leaves and birds packing more nests into their restricted territories. Further figures from contrasting colony sites are required to test this idea.
- iii. Polygamy in the Baya is based clearly upon the greater availability of potent females compared with potent males in any one season. The disproportionate sex ratio in the breeding colonies is probably due to the failure of the males to breed in their first year. However, since the sex ratio of fledgelings has been shown to be slightly in favour of males, the question remains open.

II. TERRITORY

1. General

The male Baya establishes his ownership of a particular site by loud song and aggressive behaviour (see p. 15) to all approaching birds. He also gives the nest advertisement display there (p. 22). Careful observations mostly in the Hingane colony in 1958 revealed the following facts :

- i. At least two males may build upon established nest sites up to the helmet stage ; thus neighbours build upon each other's nests

- during the earliest stage of construction. This was observed only at the onset of breeding when the first nests were being started. At this time the territorial aggressiveness of the male is least marked and territories barely established.
- ii. Defence of the site begins soon after the first stitches have been made in any selected place. The founder soon becomes intolerant of other males visiting his nest and building upon it and any attempt to do so may lead to a fight. Thereafter, males approaching nests other than their own do so in sleeked postures (strong tendency to flee) and usually make attempts to steal material for their own nests. Two nest sites may be established at once : usually they are close together, and the male may thus construct two wads at the same time. Usually one nest develops faster than the other and becomes the centre of the territory.
 - iii. Two established nests of a male may be separated occasionally by a great distance. Two cases were observed at Hingane in which the two nests of a male were situated on opposite sides of the well. The territories of these birds were thus in two parts. In both cases the double territories were maintained for a few days until one of the nests was abandoned and its site no longer visited or defended.
 - iv. Experiments (see below) show that the spatial extent of a Baya territory is compressible down to that of the nest (or the nests) itself. Thus when nests were brought very close together, the males would lunge at one another from them and show much threat, but in no case was a nest abandoned and rarely did ferocious fighting result. It is thus the nest itself rather than a volume of space of certain size around it which is significant. However, supplanting attacks are often made at neighbouring males during establishment of the territories and threat occurs at distances of between three and six feet approximately from the nest site. The distance from the nest at which a male refuses to retreat in the face of threat or attack is easily observed and marks the inner limits of a boundary zone. The territories are so packed that there is rarely any ' no man's land ' between them.
 - v. A further factor influences the size of territories. This is the frequency of suitable sites in a given area. Thus over wells, where the vegetation is sparse and the numbers of suitable twigs few and scattered, the defended areas may be large, up to several square feet. On the hanging leaves of tall palms, however, every pinna of which offers a suitable site, nests are frequently placed very close together and the territories are

much smaller as a result. It is thus partly the distribution of suitable sites that determines the number and the size of the territories within a given area. The males establish territories including as much space around their nests as their neighbours allow them.

2. Experimental compression of territories

A number of simple experiments were made to determine the extent of the defended area and changes in behaviour of the individuals concerned under modified conditions. Nests of neighbouring males were moved closer to one another and the behaviour before and after the move was recorded.

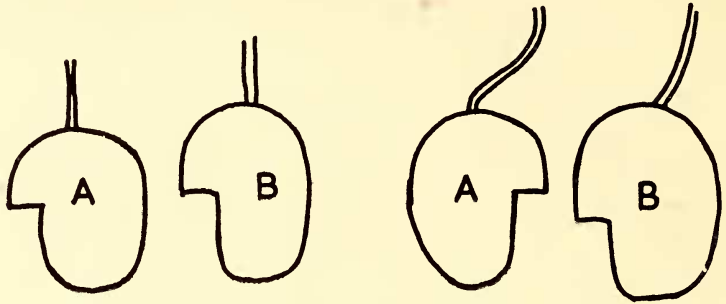
TEST I. Two neighbouring nests, A and B, originally two feet apart, were wired together with approximately one inch between them. The entrance remained in the same relative position throughout (see figure). The nests were completed egg chambers but only A was certainly accepted by a female.

For 15 minutes before the test the nests were watched closely and the two males were present on their respective nests several times. No aggressive encounter of any sort was observed between them. As soon as the change was made the two males returned to their nests and at once assumed mild threat postures (i.e. Tail depressed Threat). Bird B fixated bird A intensely but kept the body of his nest between himself and his opponent. Bird A maintained his threat posture and sat on a twig above his nest with his back to B much of the time. Whenever A hopped down to his nest, B hopped off his on to a twig, a little further from A than before, and whenever B hopped to his nest, A retreated to a twig in the same manner. Once when male A flew to his own nest, B supplanted him and twice, when female A flew to nest A, both males attempted to enter the nest (copulation attempt) after her but, after a brief supplant from male A, B retired to his own nest. Most of the time the males sat near their nests taking little note of each other. When male B was absent for a time male A made shaping movements in the beginnings of the tube on nest B and then, sitting on nest A, leaned out and pulled a small strand off nest B.

At the end of the test the nests were restored to their original positions.

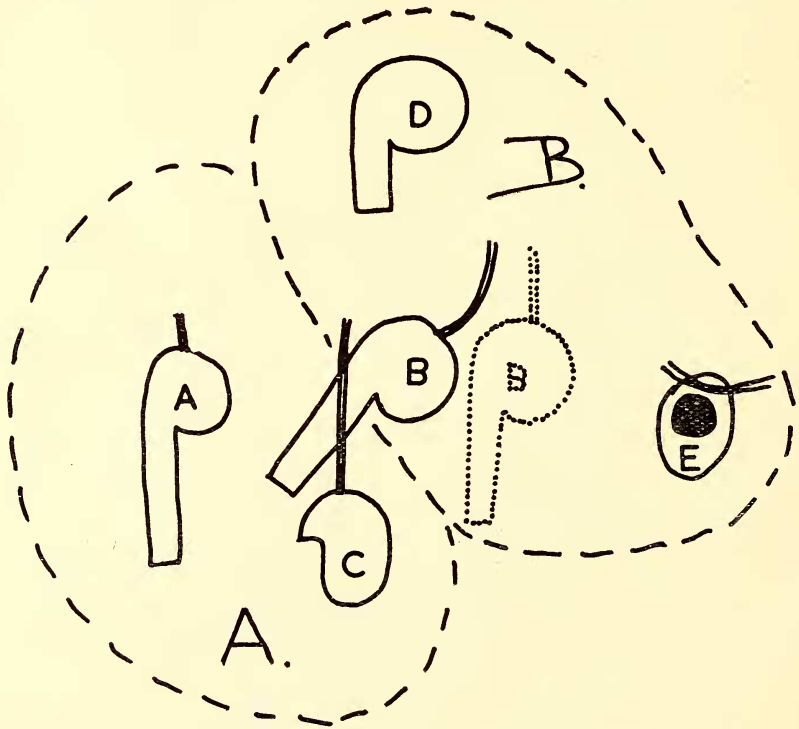
TEST II. The same two nests were wired together at the same distance but this time with their entrances close together. Male A pulled out the wire so that the nests swung apart and the experiment had to be set up again and left over night. Next morning A hopped about on both nests but mainly on A. His female entered nest A and the male displayed

there. On her emergence she entered nest B and male A thereupon sang upon it and tried to enter it in a copulation attempt. The female titivated on both nests. Later, in the absence of male A another male, very



TEST I

TEST II



TEST III

sleeked, visited both nests twice. It was perhaps B but he was not certainly present at the nests at all.

Note on Tests I and II The tests show that the territories were compressible without fighting occurring between the owners. There was, however, a very clear increase in threat, and the owners showed a strong tendency to avoid one another. Neither bird would allow the other on its nest which thus marked the limit of the compressibility of the territories. Male A appeared dominant to B, this being enhanced perhaps by his possession of a female which visited both nests in the absence of male B. In Test II, after the entrances had been apposed, it appeared that male A had taken over both nests and that, if B came at all, it was in the sleeked posture of a trespassing bird. No bird other than A showed territorial ownership at the two nests during Test II (see also Test IV).

TEST III. Two neighbouring territories, again called A and B, were chosen. Male A owned nests A (completed with tube and female) and C (uncompleted helmet stage nest with no female). Male B owned nests B (completed with tube and female), D (old completed, no female) and E (abandoned helmet stage nest). In the test the nest B was slightly tilted and wired so that its tube entrance opened into the defended area of A only two inches from the tube of nest A (figure).

Before the change no interaction (beyond one case in which male B attempted to follow female A into her nest and was supplanted by male A) between the birds of the territories was observed. Immediately after the change the following events were recorded :

1. Female B returned and hopped on to a twig, which had been previously her last perch before flying up the tube of her nest. She flicked wings and tail in obvious 'anxiety' (intention movement of flight) and repeatedly flew between the twig and the top of her nest B. She never approached the tube entrance of the nest. She then flew to old nest D and the male B followed her there and gave a full advertisement display (p. 22) upon it. Previously no female had visited this nest. Male B then approached the displaced entrance but did not enter.
2. Female B apparently located her displaced nest entrance and made two attempts to fly up into it. On both occasions male A chased her off.
3. Male A wing quivered and gave pseudo-female solicitation to female B as she hopped about anxiously on her nest (B).
4. Female A, on leaving nest A, entered nest B. Later she entered B in addition to her own nest several times. Male A greeted her with wing quivering and pseudo-female solicitation at both nest entrances.
5. Female B visited nests D and E : at D male B advertised but at E he supplanted her. Later he advertised here as well as giving further supplants.

6. Female B made further attempts to enter nest B but once more was supplanted by male A.
7. When male A was absent, female A was supplanted by male B on trying to enter nest A. Later when she flew to her nest, male B wing quivered and gave pseudo-female solicitation to her while perched on nest C. The female took no notice but flew into nest A.
8. When no other bird was present female B once arrived on the top of her nest and then flew down and entered nest A.

After forty-five minutes the nest B was restored to its original position. On returning, female B alighted on nest C and supplanted female A near it. Male B then alighted on nest B and sang ; whereupon female B at once flew to nest B and entered it. From then on the original behaviour of females A and B was restored, each going to its appropriate nest. Once, however, female B supplanted female A as the latter was going to nest A.

Note on Test III. The displacement of the nest entrance at the end of a long tube into the centre of a neighbouring territory effectively prevented both the male and the female owner from entering. The male was singularly undisturbed by the change and no aggressive encounters between him and his neighbour were recorded. The female, however, was much disturbed and made several attempts to enter her nest by passing through the neighbour's territory. On each occasion she was driven out. During her anxious hopping about the neighbouring male greeted her once with wing quivering and solicitation as if she were his own female. In addition, she visited two abandoned nests of her own mate at which he resumed typical 'Advertisement' and supplanting behaviour. In the absence of male A from his territory, male B extended his into it and drove off the former's female. Female B could then enter her own nest ; instead she actually entered that of the neighbouring female. On restoring the nest to its original position, female B resumed her original behaviour. The test showed that movement of the nest entrance disturbed the female only and that her anxious wanderings produced the following responses from the otherwise unconcerned males :

- i. The neighbouring male showed defensive supplanting and courtship approaches identical with those with which he greeted his own female.
- ii. Her own male resumed advertisement display and courtship at his more or less abandoned nest sites as soon as she began visiting them.
- iii. When the neighbouring male was absent the original owner expanded his territory to cover the displacement of his nest tube and in doing so supplanted the neighbouring female.

The return of the neighbouring male restored the defended area to its original size. Thus so long as neighbouring males are present, displacement of the nest entrances does not bring about a change in the spatial relations of their territories.

TEST IV. The following day a further experiment was carried out using the same nest group as in Test III. Nests A and B were wired together so that their entrance tubes hung a foot apart instead of three feet. Nest C was then moved to a position to the right of nest B thus bringing it into B's territory. The following occurred :

1. The two females both arrived on nest A on returning, and a fight occurred. B took nest C for her own nest and hopped on it several times until she found the B nest entrance tube and went in. Female A showed repeated threat postures at female B.
2. Female A arrived on nest B. At once female B attacked and a short fight followed before female A retired to her own nest.
3. Female B spent much time on nest C titivating it as if it were her own nest.
4. Male B titivated on nest C and hopped about on it. Male A took no notice.
5. Strong 'Tail depressed Threat' postures were given by male A when male B was in nest B. Otherwise only mild threat posturing as normally seen between neighbours was observed. When male B titivated on nest C male A fixated him but no encounter developed.

Note on Test IV. The change in the positions of the nests and the distance between them led to confused female behaviour when they returned to their territories. Fights occurred whenever they alighted on each other's nests apparently in mistake. Female B took interest in nest C formerly of A's territory but now placed in nest B's position relative to the other nests. This nest was adopted by male B and male A did not defend it. There was an increase in the frequency and strength of threat posturing between the neighbouring males.

TESTS V AND VI. In two other tests nests of two further territories were brought close together. The original distances between the nests were three feet ; after changing the nests they were at three inches and nine inches in the two tests respectively.

Results :

1. Males showed an increase in the frequency and strength of threatening in Test V.
2. In Test VI (during which the two males were never seen present at the same time) the female whose nest had been moved the most showed the greatest anxiety (e.g. wing flicking) calling and hopping about agitatedly.

3. The nests were not returned to their original positions after the tests. Aggression and anxious behaviour both disappeared after a few hours and thereafter normal territorial behaviour was recorded.

TEST VII. The young were removed from two nests and the behaviour of the returning females watched. Both became excessively anxious and visited all neighbouring nests. As these were empty no interactions with other birds occurred.

Summary of Tests :

The results of all these tests may be summarised as follows :

(1) If occupied nests are moved closer to one another during brooding there is an increase in threatening behaviour between the neighbouring males.

(2) If the entrance tube of an occupied nest is tilted so that it opens within a neighbouring territory, the owner female is prevented from entering it by the neighbouring male. The male owner does not attempt to defend the entrance tube of his nest when the neighbouring male hops on it or the female enters it.

(3) If unoccupied nests are moved into a neighbouring territory or placed near another male's nest they change owners (Tests II and IV).

(4) Displacement of nests confuses the females who follow regular routes and use certain landmarks in locating them. They become very anxious showing wing flicking, calling, and visiting several neighbouring nests. This results in fights between the various female nest owners. Neighbouring males respond to the wanderings of females with supplanting attacks or occasionally with sexual 'greetings' both of which the females avoid.

(5) When unoccupied nests are kept with reduced distances between them, the aggressive responses gradually fade until finally the interactions between the two pairs do not differ from those of birds in territories in which the nests have not been moved. The birds thus adapt themselves quickly to a much reduced territory size.

(6) The defended area can be reduced to little more than the nest itself. The arrival of strange or neighbouring birds on a nest is never tolerated.

III. AGONISTIC AND TERRITORIAL BEHAVIOUR

1. Behaviour in flocks

Baya weavers are 'Distance' species (Hediger 1950) and maintain an 'individual distance' when moving together in groups. Each individual prevents another coming near it by aggressive or fleeing behaviour depending upon the relative dominance of the two birds in the encounter. In caged groups stable 'peck right' hierarchies are established but in wild

flocks it is unlikely that the group composition is sufficiently constant for individuals to learn to recognise one another enough for this to occur. The dominance shown by one bird to another in a wild flock is thus not likely to be learnt in relation to the opponent. It is rather the expression of the innate relative dominance of the two birds. The actual tolerance distance around an individual within which another individual is never permitted is small, being about two inches, depending on the mood of the bird. It thus resembles distances estimated for other Weaver species in aviaries in Cambridge and in Senegal (Crook 1958).

The typical threat posture, composed of components that are intention movements of attack and escape, is the 'Head forward Threat' (Hinde 1953). Components indicating the tendency to attack are the crouched posture, the head held low, forward, and often rather pulled back into the shoulders, and sometimes a spread tail. Components showing a tendency to flee are the sleeking of the body plumage and a turning away from the opponent. The most frequent form of attack is the 'Supplant' (Hinde 1952) in which a bird fixates another, often in the Head forward Threat posture, and then flies directly at it and takes its perch as it flees. If it does not flee, a short fight occurs. 'Supplants' are frequent at food sources, at another bird when it has some nesting material, and in any competitive situation. Another aggressive movement, the 'Lunge', is a brisk reaching-out at the opponent as if to peck it, accompanied by an aggressive chatter. It occurs often during 'individual distance' encounters on perches, the birds then separating out and so increasing the distance between them. The 'lunge' may end in a peck in which the opponent's plumage is seized in the beak. This often starts a fight.

2. Agonistic behaviour in territorial defence and courtship

Once a male has established himself in a territory, his aggressive postures are used both in territorial defence and in the various encounters occurring outside the colony in flocks. The Head forward Threat and the Lunge are now frequently associated with the loud wheezy song which functions here in claiming ownership of the site and in warning other males to keep away. At wads, initial rings, and early helmet stage nests, the males threaten their neighbours primarily by supplanting those that come close (about three feet from the nest in a palm tree colony). Birds that hop near the borders of a defended area are treated to a loud song and much ocular fixation, the owner advancing towards them and eventually supplanting or relaxing depending on whether the other bird retreats or not.

When the helmet stage of the nest is reached and most neighbours know each other well, a further threat posture the 'Tail depressed

Threat' appears. The components are : (i) Body plumage slightly fluffed, (ii) head lowered, retracted into shoulders, (iii) tail very depressed and spread, and (iv) song or aggressive chatter. Interpretations of the motivation of this posture have been published previously (Crook, in press *a* and *b*). It arises in situations in which a sexually motivated bird is also tending to respond to an intruder with both attack and escape. It is most common in weaver species with small territories such as the *Quelea*. In the Baya the posture appears most commonly in courtship when the female has partially accepted the male's nest and the dominance-subordination relationship between the sexes is changing in favour of the female. The male then begins to show a tendency to flee from her as well as to attack her ; this is expressed by the fluffing of the body feathers (i.e. thwarted escape found in many submissive postures also). The lowered head drawn back into the shoulders, the spread tail, and the calls are aggressive while the depression of the tail, especially frequent in aggression against the female (see Table V), appears to express attack and sex together.

The exact contexts of 228 sequences of aggressive behaviour are shown in Table V. A glance at the totals of sequences for each context shows that the highest number (32.5% of the total) occurred when the male attacked or threatened the female following nest invitation displays and the female's initial approaches to the nest. In these sequences the male mostly lunged at the female (95% of the cases in the context) and in the remaining cases he supplanted her. The greater number of lunges over supplants is due to the close proximity of the birds at the nest during the invitation sequences. In addition, the male is at the time showing alternating tendencies to approach the female, either in a mounting attempt or in an attack and to flee from her. Due to this conflict situation the male's lunge rarely develops into a full attack and few supplants are seen for the same reason. In courtship, following acceptance of the nest, the behaviour is less confined to the nest and supplants leading to sexual chases are more common than lunges. Large numbers of aggressive sequences were also seen when males passed near the territory (mostly supplants, 79% of cases in context, or a few Tail depressed Threats always given to well-established neighbours, 21%) and with females, during courtship sequences, when many Tail depressed Threats (37% of sequences in context) were seen in addition to the many supplants (58%). The numbers of sequences in other contexts are also given in Table V.

Of the different types of aggressive response 91% of the lunges occurred as the female approached an advertising male. The majority of supplanting attacks was given against approaching males (33%) or neighbouring males in display (26%) with a further high number occurring during the courtship sequences (19%). Tail depressed Threat occur-

TABLE V

The occurrence of the three main types of aggressive behaviour of male *Ploceus philippinus* in differing contexts in territorial defence and pair formation.

Contexts	Aggressive Responses			
	Lunge (i.e. Head forward Threat with attempted peck)	Supplanting attack	Tail depressed Threat	Total of sequences per context
Strange male at the nest	..	9	..	9
Neighbouring male in full display in nest advertisement ; no female present	2	25	2	29
Neighbouring male in full advertisement display ; female near attacker's nest	..	8	..	8
Another male passes close by nest	2	43	9 (to neighbouring birds)	54
Attack on female during nest invitation (i.e. following her arrival after the advertisement display)	67	7	..	74
Attack on female during courtship	2	25	16	43
Strange male attacked while at a neighbour's nest	..	8	..	8
Aggressor attempts to rob material being carried by another male	..	3	..	3
Totals of sequences	73	128	27	228

red most commonly in courtship sequences (59% of cases observed). Eight supplants were seen against strange males visiting nests belonging to the neighbours of the defender. In this case the latter sallied forth from his territory to defend a neighbour's nest in his absence. It seems that the sleeked appearance of male strangers encourages attack even from a distance beyond the territory. In this way males sometimes save the nests of their neighbours from robbers. Owners of nests at

which a female was visiting sometimes attacked neighbouring males who were advertising near by (8 cases). However, since the owners in such contexts are primarily occupied with the female the number of aggressive responses to near-by males is much less than when a group of males displays together in the absence of a female (29 cases).

3. Discussion of agonistic postures in pair formation

Supplants are shown by birds motivated by an unopposed attack tendency. Lunges, when they develop into a pecking attack, may be interpreted in the same way but in most cases the lunge does not reach the target and the bird often withdraws. Lunging thus is usually part of a posture or sequence in which attack and escape response tendencies are in conflict. We have already seen that they may be given to both males and to females. In the Tail depressed Threat attack, escape, and sex tendencies are all activated. The majority of these postures occur in response to the female in courtship sequences. Nevertheless they also play an important role in territorial defence against neighbouring males once the nests have been well established. This is presumably because the posture has acquired value as a social signal proclaiming ownership of a nest and territory during the course of its evolution and ritualisation (further discussion in Crook, in press *b*).

4. The occurrence of song

The loud wheezy song is heard in the following contexts :

- (1) Given by several males in concert while resting in a group. Often it occurs during bouts of preening or sitting drowsily and well before breeding commences. Thus loud singing may be heard in groups in day roosts in March and April. The song is not orientated at any other individual nor does the song posture reveal any component associated with attack tendency.
- (2) Males may sit in their territories and sing without orientation to other individuals and without attack tendency present.
- (3) Song may be given at males approaching or near the territory. In these cases the posture includes threat components (e.g. rump fluffing, tail spreading) and the bird faces the opponent.
- (4) After giving a supplant the male may return to his territory and sing.
- (5) The males repeatedly sing to females after their arrival at the

nest. Such songs are given during the performance of 'wings rigid' posturing (p. 22) and in the post-courtship phase after abortive threats. They are often given on the exterior of the nest, the female being within.

In (1) and (2) there is no aggressive motivation apparent and no reason to suppose its presence. Song increases as the breeding season approaches though it appears to be present to some extent throughout the dry season. Thus caged hand-reared juveniles sing when a few weeks old though the song is not yet fully formed. Song is evidently associated with sexual motivation and its repetition in choruses, in which social facilitation plays a notable role, may possibly bring about a synchronisation of the timing of maturation so that all birds are physiologically ripe when environmental stimuli elicit breeding. In (3) and (4), however, song is occurring in aggressive contexts and functions in announcing the ownership of a site and thus as a warning to neighbouring males. In (5) too the context is aggressive though sexual motivation is usually apparent at the same time. It is unlikely, therefore, that the song plays much part in attracting the female and, further, the vocalisation accompanying the advertisement display is totally different (p. 22). Song is most marked, except in (1) and (3), where there is a conflict between two or more tendencies and where the tendency to attack is especially strong.

IV. NEST INVITATION, COURTSHIP, AND HAREM FORMATION

1. The pair formation process

In common with many other Ploceine species the pairing process of the Baya falls under two headings: (i) nest invitation by 'advertisement' display, and (ii) courtship. As soon as the nest reaches the 'ring' stage, the 'advertisement' displays are given upon them, although usually not at the full intensity achieved later on helmet stage nests. The display (see below) consists in a vigorous wing beating given while hanging below the nest and clearly functions in attracting the female. Courtship posturing follows the arrival of a female at a nest with which she is already familiar following frequent previous visits. The male's initial hostility to her wanes; he begins to court her, and she shows sexual solicitation in return. Copulation eventually results. After egg laying, throughout brooding and the rearing of the young, several courtship postures are retained as part of the greeting ritual shown mutually by the birds whenever they meet at the nest. These postures may also lead to copulation even when the young of the pair are well grown. The courtship postures, in modified form, are found throughout the entire occupation of the nest by the female and her family.

Before describing the details of these behaviour patterns and sequences, the changes in the mutual behaviour of male and female in the territory at different periods in the annual life of the colony may be summarised.

A. Preliminary breeding attempts (i.e. after the first early showers of the monsoon)

- i. Nest as a wad or ring. The male's responses to the female's approach are at this stage primarily aggressive. Advertisement displays may be given as a result of social facilitation with the displaying of other males on more advanced nests near by ; they are never long sustained.
- ii. Nest at helmet stage. Prolonged and excited advertisement displays follow the arrival of a female or group of females in the colony. When the female approaches and enters a nest, the owner responds with courtship but copulation does not yet occur nor does the female solicit. The male frequently becomes very aggressive towards the female as soon as she alights on his nest, even though this may follow several minutes of ardent invitation. The nervous female flees at the slightest provocation.

During these preliminary breeding attempts activity in the colonies is only sustained for a few days. It then rapidly wanes and the place becomes once more deserted until further showers of rain are accompanied by renewed activity.

B. Definitive breeding season.

As soon as definitive breeding starts the above activities are again observed at wads, rings, and helmet stage nests. Now, however, the nests are constructed beyond the helmet stage following their acceptance by the female.

PHASE I

Nest as a completed egg chamber : Nests of this stage have been accepted by the females and courtship occurs on and near them at maximum intensity. Whenever the females fly from the nests the males chase them for considerable distances outside the

colony and the females lead them back to their nests. At the nests the females solicit and the males copulate with them. The females also frequently refuse to copulate and attack the males instead. In such sequences the males often give the pseudo-female solicitation postures which form a marked element in courtship. As a female becomes established at a nest site advertising becomes rarer though it is maintained at the fresh nests in the territory.

PHASE II

Eggs in the nest :

Females visiting the nests for brooding are greeted by the males with much wing quivering and often pseudo-female posturing. Copulation can still occur.

PHASE III

Young in the nest :

Greeting behaviour becomes less frequent as the male remains in his territory for shorter periods. He also often assists in feeding well-grown young.

PHASE IV

Young away from colony :

Both parents feed the young after they have left the nest. No courtship or greeting postures have been seen between the sexes at this time.

2. Nest invitation and the early courtship sequences

Females are not present in the colonies at their establishment. The males busy themselves building, robbing each other's nests of material, supplanting one another and indulging in bouts of singing. The females first appear either singly or in small groups flying swiftly into the colony, hopping rapidly about the branches in very nervous sleeked postures, and occasionally flying up to a nest or two giving them apparently a brief inspection. The males with wads or rings usually react aggressively to the females' approach, threatening them and making short swift supplanting attacks. Males with helmet stage nests react strongly to the females' arrival giving intense 'Advertisement displays', hanging below their nests, and a particular call. Between displays they hop about wing quivering intensely and repeatedly fly back to their

nests for further displays. The males advertise either with the female present near the nest or when stimulated by the displaying of neighbouring birds. Thus even if only one or two females have entered the colony many of the males burst out in display immediately. Birds with wad or ring nests usually only quiver the wings or sometimes continue their building without responding to the females. The displays clearly attract the females for they rarely approach nests earlier than the helmet stage, and confine their attention especially to those upon which the males display.

The Advertisement display has two main forms, the Wings beating Display and the Wings rigid Display. Both displays are associated with much wing quivering which frequently precedes a bout of display. The Wings beating Display is given on the nest or on twigs near it. On the nest the males usually perform upside down but on twigs the body is normally upright. Wings beating Display is given during the female's approach and prior to her arrival but the Wings rigid Display is given immediately she alights on the nest. One can thus observe a transition from wing beating to the rigid posture on the arrival of the female.

The Wings beating Display has the following components :

- (1) The bird hangs from the nest, usually positioned on the developing roof of the egg chamber. Frequently the line of the back is inclined at an angle of 45° to the vertical, but often the bird is completely upside down with the back horizontal.
- (2) The wings are fully spread and hang down below the back. When the display is given in the 'upright' position the wings are of course extended and raised above the body.
- (3) In either case the wings are beaten at a speed of about 10 beats per 1.8 seconds (Table VI) through an arc between approximately 45° and 135° to the dorso-ventral plane of the bird's body.
- (4) The tail is slightly spread and either held in line with the back or slightly depressed upwards against the fabric of the nest.
- (5) The birds emit a continuous call rendered *wheetu wheetu wheetu* or *che weee che weee che weee* in the field notebooks.
- (6) The beak is often held down against the breast during display or the bird may peer around after other birds.

On the female's arrival the display changes to the Wings rigid Display through the successive development of the following components :

- (1) The bird remains hanging on the nest in the same position.
- (2) Wing beating ceases totally and the wings are held stiffly out

at the side of the body at between 45° and 90° to the dorso-ventral plane of the body.

- (3) The tail remains spread.
- (4) The feathers of the crown are raised.
- (5) The bird leans forward slightly towards the female, often peering under the edge of the nest wall and sings loudly.
- (6) As the bird leans forward with the crest raising, the wings are usually synchronously relaxed to the side of the body, a movement usually complete as the song begins.

During the initial approaches of the females the males' responses were closely observed on 154 occasions. During 50 of these the female remained near the nest but did not approach it closely, while the male merely quivered his partially extended wings. On 104 occasions the females came exceedingly close to the nests and the males gave the Wings beating Display often coupled with short flights down towards the female where they perched on twigs and gave either wing quivering or upright Wings beating Displays. In 74 cases the female alighted on the nest and the male responded with the Wings Rigid posture, a song, and often an attempt at pecking the female. A large number of these sequences were tape recorded and are shown in Schemes A, B, and C.

While visiting the colony the female is sleeked and nervous, showing a strong tendency to flee. She darts from one position to another, being frequently supplanted by the males and chased by them. Finally she alights in the nest of a displaying bird and, maintaining her very sleeked plumage, makes shaping movements in the cavity. As soon as the male threatens she flees.

3. Nest acceptance and pair bond formation

The females clearly make a choice of the nest they are to occupy for although at first they may visit several nests they soon concentrate their attention on one nest only and no longer visit others. It is difficult to gauge how far the female is affected by the male's displaying in making her choice of nests and how far it is the nest structure itself that counts. The fact that females only accept nests that have reached the helmet stage suggests that the structure itself plays the more important role though it is likely that nest structure and the male's performance taken together combine in influencing the female. However, once a female returns persistently to any given site the behaviour of the male undergoes a change and courtship rather than advertisement becomes the chief activity at the nest.

The change in behaviour occurs gradually. The original short supplanting chases whereby the male drove the female from his territory become more sustained and the male may pursue the female outside

the colony. After these long chases he may at first return alone but eventually the female, after leading the pursuing male in a long detour up to several hundred yards around the colony, flies straight back into

TABLE VI

Wing beating speeds in the Advertisement Displays of *Ploceus philippinus*
(Stopwatch accurate to 0.1 second)

Time taken for ten wing beats in seconds	Number of cases observed
1.4	1
1.5	4
	} 5
1.6	3
1.7	4
	} 7
1.8	14
1.9	4@
	} 18
2.0	12
2.1	4
	} 16
2.2	2
2.3	0
	} 2

@ This reading is due clearly to some subjective bias for reading 1.8 or 2.0 rather than 1.9 on the stopwatch dial.

it and alights in the male's nest. The chases lose their aggressive character and become interwoven with other courtship activities, the motivation of the chase becoming, at least in part, clearly sexual. The male may now make attempts at mounting the female, attempts at which the latter at first reacts aggressively, lunging or fiercely threatening the male. The chases are interpreted as prolonged attempts at mounting. During these sequences a change in the relative dominance of the two birds occurs so that the male can no longer dislodge the female from his nest so frequently. Thus whenever the male turns aggressive the female often pecks back with such effect that he desists and sits disconsolately near by until, as she flies off in her own time, he chases her. In scheme A these later sequences are marked with an asterisk.

By this time the nest is nearly finished. The usual sequence of events in the territory is summarised below :

- (1) The female alights in the nest entrance. The male, who may have given a few wing beating movements, usually sings

and then makes repeated attempts to enter his own nest. Some of these attempts are highly aggressive but the majority are attempts at copulation. The female refuses entry to him and when she departs he chases her.

- (2) Ultimately, however, the female responds to the male's constant advances with solicitation and, although in many cases this turns again to threat as the male approaches, it ultimately ends in a successful copulation.
- (3) At this time the male's sexual excitement is very evident. Apart from occasional bouts of aggressive behaviour, he is constantly wing quivering and approaching the female in short flights attempting to mount her. As the female is usually positioned in the ring entrance of the nest most of the attempted copulations occur there, but they also occur on other parts of the nest or on twigs near by. If the nest has a fully completed egg chamber and the start of a tube, then the male attempts to mount the female as she is sitting on the cross bar of the nest (the former perching position in the base of the initial ring of the nest frame) within the base of the tube. Such cases may be observed by tilting the nests so that the observer can see up the tube. Many of these attempts fail as the female repeatedly turns on the male and drives him off.
- (4) Under intense sexual frustration (i.e. following repeated rejection of his advances) the male gives pseudo-female solicitation, thereby soliciting the female in exactly the same postures as those whereby she solicits him.

In these copulation sequences the behaviour is extremely variable. The male's wing quivering advances may be met with an immediate crouching of the female and copulation may then follow immediately. Usually, however, the female resists the male's approaches with some degree of aggression alternating this with spells of wing quivering in concert with him. When the female solicits copulation normally follows at once, but when the male solicits the female usually responds only with wing quivering. She may also solicit, however, in which case again copulation is the normal consequence. The process is highly elaborate and the male by constant wooing provides the stimuli that elicit the female's sexual responses thereby suppressing her tendency to attack. The female's sexual behaviour (soliciting, etc.) elicits the male's responses and results in copulation.

Solicitation by the female has the following components :

- (1) The body is deeply crouched and the breast especially lowered,

the feathering of the breast and body being often slightly fluffed.

- (2) The wings are drooped slightly but only a little spread. The initial wing quivering that normally precedes solicitation gives way to extremely high speed tremoring most noticeable at the wing tips.
- (3) The tail is slightly raised and tremored in the vertical plane at high speed.
- (4) The head may be slightly tilted backwards and the beak thus points upwards.
- (5) Crown and nape slightly fluffed.

The components of the male's pseudo-female solicitation are closely similar to the above though the body is rarely so deeply crouched and the head is less prominently tilted. In the male's display wing quivering with fluffed body plumage changes to pseudo-female solicitation by an increase in the speed of the wing movements with a marked decrease in their amplitude. At the same time the tail is slightly raised and tremored at high speed. When giving this posture the male frequently gives a special cry, a high pitched *ti ti ti ti t t eeee* which also accompanies the act of copulatory mounting. Also when highly excited the male may clipper his mandibles together producing rapid little snapping sounds. This happens particularly when the male is flitting after the female in the territory, much fluffed and wing quivering and obviously highly motivated sexually.

When the male mounts the female prior to copulation she crouches in solicitation and her tail often keeps up the high speed tremoring. She then raises her beak and points it up vertically. The male then lowers his cloaca to make contact with that of the female who raises her rump and puts her tail to one side. The male utters the copulation call and flutters his wings throughout. After copulation the pair usually separate and the female is very prone to attack the male. Often, however, she flies rapidly out of the colony leaving the male hopping about often wing quivering. The female has been observed making washing movements with the wings after a copulation.

4. Analysis of behaviour sequences during courtship with comparisons with other colonial weaver birds

In Scheme A behaviour sequences recorded during nest invitation are drawn to reveal the variety of responses that occur. In Scheme B

and C sequences of male and female behaviour respectively are shown during courtship and copulation. Nest invitation and courtship do, of course, merge into one another but their separation in the Schemes is justified because there is in fact a considerable and fairly abrupt change in the behaviour of the birds as soon as the female comes repeatedly to the nest and thereby demonstrates her acceptance of it. Nest invitation displays thereafter become less frequent and intermingled with a far greater frequency of courtship sequences. In addition, acceptance of the nest marks a major change in the male's building activity. The nest is at first rapidly constructed up to the helmet stage and then maintained without further change of form until a female has accepted it. Thereupon the male resumes construction at high speed completing the nest chamber in time for the laying of the clutch. The tube is only added during the laying and early brooding. The change in behaviour was shown clearly on 12 August 1958 when a count of Wings beating Displays during a set observation period gave 44 on helmet stage nests but only 7 on nests with recently completed egg chambers.

An individual male may have several nests at one of which courtship is in full swing while at another he may give Advertisement Displays. Thus at any one time in different territories some males are advertising, others courting, and others doing the former at one nest and the latter at another. At the Hingane colony this mixture of behaviour persisted from 6 August to 10 August 1958 approximately by which time most females had commenced laying and the majority of nests had been accepted. Throughout the whole life of the colony, however, there were some males with helmet stage nests at which they continued to advertise long after fresh females had ceased prospecting and while their other nests contained well-grown young.

A. Nest Invitation

Sequences following 141 arrivals of females in the colony (Scheme A) show that 94 (66.8%) were followed by Wings beating Displays by the males at helmet stage nests, 16 (11.3%) by threat at helmet stages, 16 (11.2%) by vigorous supplants and chase by the male, and 14 (10%), in which female approached wads or rings, by threat. The male thus reacts with aggression more particularly at wads and rings. As soon as the nest reaches the helmet stage he gives Advertisement Displays. Thus from treating the female primarily as an intruder to his territory the male begins responding to her in a manner that encourages her approach (i.e. wing quivering and Wings beating Display).

The sleeked, dodging-about behaviour of the female clearly encourages the supplanting attacks of the male; yet it is clear from the start

that females are to some extent recognised as such. Thus the tremendous excitement generated in the colony by the arrival of one or two females demonstrates that the birds are in no way confused with other males. Further the large amount of wing quivering occurring between pursuits and while the male is not actually displaying is a well-known component of sexual behaviour. The initial appearances of the female near the nest thus elicit both aggressive and sexual responses from the males. The females show a strong tendency to flee (constant crouching in take-off postures, frequent wing flicking, and extreme sleeking of the body plumage) yet in spite of this the tendency to approach the nests and to examine them (undoubtedly an aspect of the sexual tendency even though courtship wing quivering and solicitation is not at this time observed) brings them repeatedly back to the colony.

The Wings beating Display is most complex. In two other colonial weavers (*Ploceus cucullatus* and *P. castaneofuscus/nigerrimus*) in West Africa homologous Advertisement Displays have been analysed and discussed at length (Crook, 1958, in press *b*). The Baya's display resembles these closely and a full analysis of its motivation will not therefore be given here. But the following points are made by way of explanation and to show the differences in the nest invitation of these three very similar species :

1. The Wings beating Display is a complex posture in which components derived in evolution from sexual chasing (wings beating) and song bowing (tail spreading and depression, beak against breast) threat postures are combined into a partially 'ritualised' static display given on or near the nest.

2. The component composition of display shows that the male is responding with attack, sex, and escape all at the same time. So long as the stimulus situation provided by the movements of the female remains relatively constant, the conflicting tendencies remain in the same effective ratio to one another. They then appear in the typical intensity, frequency, and form of display.

3. As soon as the female actually alights on the nest the male *P. philippinus* gives the Wings Rigid posture. In *P. cucullatus* the same thing occurs but it is followed immediately by 'dashing to and fro' within the territory during which he makes frequent visits to the nest where he bows to the female, sings to her, and may lunge at her. This has been interpreted as an initial freezing of the display with the tendencies to attack and to escape from the female effectively equal, followed by alternating movements of attacks and escapes or threats at the female at the nest. In *P. castaneofuscus/nigerrimus* the male usually wing quivers or droops his wings before 'dashing to and fro'. This

is interpreted as a strong sexual response in conflict with escape, there being comparatively little attack motivation apparent. Contrasted with these, the Baya's display changes firstly to the Wings Rigid posture and then passes immediately into a threatening song bow towards the female. Of the components of the display the cessation of beating and the rigidity of the wings represents the initial 'freezing' of wings beating with the attack and escape tendencies in balance and cancelling each other's manifestation; the spread tail, occurring otherwise in threat postures, indicates the presence of the tendency to attack; the raised crest, occurring otherwise in alarm, indicates the tendency to flee; the fixation of the female and the leaning forward are preparatory movements of lunging and, together with the spread tail and the song, reveal the tendency to attack; the relaxation of the wings (component 6 on p. 23) indicates the absence of intention movements of flight.

4. All this indicates that the reaction of the Baya to the arrival of the female is primarily aggressive but that the tendency to attack is *at first* partially inhibited by the opposing tendency to flee. This interpretation (for further discussion of the analysis of components in these displays see Crook, in press *b*) is supported strongly by the subsequent events in the behaviour sequences shown in Scheme A. Thus following 74 Wings Rigid postures the male actually pecked into the nest at the female 57 times and in all but 7 cases (3 in which the male relaxed on the departure of the female and 4 in which the female threatened him) he finally chased her from the nest as she fled. Only later after much chasing (an activity that is less prominent in both the West African species) do sexual responses appear at all clearly (Scheme B).

From this account we see that the differences between the displays of the Baya and those of the two West African species are due to the relatively more aggressive responses of the male to the first approaches of the female. The female Baya also is a more aggressive creature than the female of the other two species, and only after much threatening and chasing do the birds become sufficiently accustomed to one another for mutual sexual behaviour to become possible. The aggressive nature of the female also accounts for the high incidence of pseudo-female solicitations shown by the male Baya late in pair formation. The sexual chase plays an important role in courtship. It develops out of supplanting attacks through the gradual appearance of sexual responses and late in courtship the chases are inextricably part of the pairing process, the female leading the male back to his nest where she often solicits him. The Baya differs from *P. cucullatus* and *P. castaneofuscus/nigerimus* markedly in this respect and resembles other species [e.g. *P. benghalensis* and *P. manyar* in India and *P. (Xanthophilus) aurantius* in West Africa] in which sexual chasing plays a prominent role in court-

ship and nest invitation. Hinde (1953) discussing the sexual chasing of the Chaffinch (*Fringilla coelebs*) and other birds suggests that it may have a stimulating effect on the female. This is certainly so in the Baya where the female returns to the nest after a chase and solicits (Scheme C).

It has been suggested elsewhere (Crook, 1959, in press *b*) that, in the evolution of complex colonial life in certain weavers, highly motile displays in both territorial defence and nest invitation have given place to static posturings derived from the earlier movements. *P. cucullatus* and, as recent work has shown (Ali & Crook 1960), *P. megarhynchus*, in which territorial defence is conducted largely by immobile posturings and in which the sex chase is virtually absent in courtship, are the most advanced species in this respect so far observed. The Baya seems to lie between these two, together with *P. castaneofuscus/nigerrimus*, on the one hand and less colonial species on the other. The implications of these comparisons will be developed further in a later publication, by which time further species will have been studied.

B. Courtship

The behaviour sequences of the male and female during courtship are summarised in Schemes B and C respectively and the wide variety in the male's responses clearly shown (headings A-G in the Scheme). 51% (24 out of 47 cases) of the sequences in Scheme B show the male attacking or threatening (sequences passing via headings A, B and C) while the remaining sequences (23), amounting to 49%, show sexual motivation predominant. The relations between sequences under headings C and D show that initial aggressive behaviour may change easily to courtship at least for a time. Out of 23 cases in which courtship began well only 7 resulted in a successful copulation (30.5%) though a further 8 mounting attempts were made (34.7%) in which the female fled. In a further five cases (21.7%) the female reacted aggressively to the male's approaches and in one case fled in the course of courtship. In no case, where the sequence began with aggressive behaviour or included it, did a mounting attempt occur. The same situation is shown in the sequences of female behaviour, complementary to those of the males, presented in Scheme C. An attack tendency thus precludes the possibility of mating and, in a situation in which so much aggression is shown by both sexes, the frequency of sequences in which both sexes are sufficiently motivated sexually and reacting mutually without aggression is notably small.

The postures given by the birds in these sequences are mostly simple when compared with those of nest invitation. They are likewise com-

posed of components representing the tendencies to behave sexually, to attack, and to flee. Thus in the sequences under headings A to C in Scheme B the tendencies to attack and to flee are seen in conflict. The postures may later incorporate typical sexual components such as wing quivering, and with a further increase in sexual motivation, change to postures containing sexual components alone. Under the headings D to G sequences occur in which the sexual tendency is in conflict with the tendency to flee, though here again aggressive behaviour is recurrent. The significance of most of the postures shown has been discussed elsewhere (Crook, in press *b*) so that only a summary of their interpretations need be given here :

1. Wing quivering. Given by both sexes.
 - Motivation. It is normally associated with and precedes sexual behaviour in many passerine birds (Hinde 1952, 1955-56, Marler 1956, Andrew 1957, Crook, in press *a* and *b*). Some escape motivation is also present.
 - Derivation. It appears to be derived from the wing quivering of juvenile birds (Marler loc. cit.).
 - Function. It is often associated with submissive 'fluffed' postures and it appears to reduce the likelihood of attack from birds approaching or approached (e.g. as in courtship and in food solicitation by juveniles to adults). It allows partners to approach one another closely prior to mounting.

2. Solicitation. Given by the female.
 - Motivation. Largely sexual though the crouching component, an intention movement of flight, suggests the tendency to escape (Marler, loc. cit.)
 - Derivation. Movements of copulation and preparatory movements of flight.
 - Function. Invitation to the male to copulate.

3. Pseudo-female solicitation. Given by the male during copulation sequences and in the post-courtship period. It begins with the first copulation attempts following the acceptance of the nest by the female and thus coincides with the shift in relative dominance in her favour.
 - Motivation. The sexual tendency is in conflict with a strong tendency to escape. Thus it is not found early

in courtship when the male is dominant and highly aggressive. It follows threat by the female and when the male leads the female to the nest (Scheme B, headings E and G).

Derivation. The posture consists of preparatory movements of copulation and flight and evidently shares common causal factors with female solicitation (Hinde 1955-56, p. 15).

Function. Probably the same as wing quivering. It appears also to elicit solicitation by the female. The posture has been observed in many weavers but rarely so frequently as in the Baya. The high level of aggression shown by the female which produces frequent thwarting of the male's mounting attempts is responsible.

V. THE MUTUAL BEHAVIOUR OF MALE AND FEMALE FOLLOWING PAIR FORMATION

Once the pair bond is established and courtship over, the females and males occupy themselves respectively with brooding and the courtship of further prospecting females. In addition the male is zealous in strengthening his nests, in lengthening the tubes, and in defending the territory against the depredations of robbers. The male remains most of his time in the territory, and thus established females frequently encounter him on their journey to and from their nests.

When the two birds meet, a number of alternative sequences may be observed. These are set out in Table VII where the female's behaviour on entering the nest is matched against the male's response. A glance at the totals reveals that 36.6% (i.e. 37 of 101 cases) of females arrived and flew to their nests without showing any particular posturing, 34.6% solicited their mates, 14.9% wing quivered before entering, and 9.9% solicited or wing quivered (35, 15, and 10 cases respectively) even though their mates were at the time not present in the territory. A remaining 4% solicited neighbouring males in the absence of their own. Correspondingly, of the males' responses 33.8% were pseudo-female solicitations (30 times out of 91 cases)¹, 20.1% wing quivering (19 times), and 10.9% aggression (10 cases), i.e. flying to the female at the nest and singing loudly sometimes with lunge, or supplanting. 63.3% of the

¹ On one occasion a male was observed giving pseudo-female solicitation to a male flying past, apparently a case of mistaken identity.

males' pseudo-female solicitations were given to those females that flew directly to their nests without posturing, merely perching a moment and wing flicking (intention movement of flight) before darting up the tube (19 of 30 cases in context), and 33.3% to females that were themselves soliciting (10 cases). Females that wing quivered were solicited by the male rarely and were usually met with wing quivering. Occasionally other neighbouring males also joined in the wing quivering though without approaching near enough to invite an attack from the owner (4 cases). The frequency with which wing quivering was met by the same behaviour in response, and soliciting likewise with soliciting suggests strongly that the male, if he responds, tends to show a similar behaviour pattern to that of the female. However, the male often showed no response at all (26.2% of total male responses) and especially to soliciting females (45.7% of responses in context); yet only in 5 out of 37 cases (i.e. 13.5%) did the male fail to react to a female flying directly to the nest without posturing. Here it is noteworthy that of all the male's aggressive responses 60%, including all four observed supplants, were made against females that showed neither wing quivering nor solicitation on entering the territory.

It is thus clear that, in addition to aggressive responses, courtship postures and solicitation persisted well after the period of their greatest significance during pair formation. The male solicited established females both when they solicited him and when they entered the territory in a sleeked manner. A number of such encounters led to mounting attempts and even to a few apparently fully competent copulations. Some of these took place at a time when the females concerned were actively engaged in feeding young. Both sexes are thus fully potent sexually for a long time after the initial pair formation. Often the male responds to his established female as if she were a prospecting newcomer and especially so if she enters the territory without greeting him (Table VII). Her sleeked posture and wing flicking then resembles the nervous behaviour of a prospecting bird. Sometimes an established female returning in this way is met with advertisement display on the latest helmet stage nest thus suggesting that the male is responding primarily to her posture and that her identity as an individual bird is indistinctly known by him. In a few cases the established female actually responds at once to the male's invitation and visits the nest, pokes about in it, is threatened by the male and so on, exactly in the manner of a freshly arrived bird, and often with food in her beak for the young all the time. Thus not only is the male liable to attack his female and invite her to a fresh nest but the female may also respond with appropriate behaviour, but in relation to her functional role at the time, certainly out of context. All this again is set against the background of repeated threats by the male. We have seen that females entering the territory without

TABLE VII

Tabular representation of behaviour sequences of females and males in territories during brooding and care of young in the nests. (The sequences follow the arrival of the female in the territory. The numbers of male responses recorded are placed against the behaviour of the female on her arrival.)

Behaviour of female on arrival in colony	Male						
	No of sequences observed	Male supplants female	Male gives no response	Male flies about nest, wing quivering	Male flies to or near nest; sings at female	Male gives pseudo female solicitation	Strange male wing quivers with ♀.
Female flies to nest without posturing	37	4	5	7	2	19	..
Female approaches nest, wing quivers to her mate	15	..	3	6	1	1	4
Female approaches nest soliciting her mate, often carrying food for her young at same time	35	..	16	6	3	10	..
Female approaches nest and solicits a male other than her own near her nest; own mate absent at time	4	4
Female in territory in absence of mate nevertheless shows wing quivering or solicitation	10 (7 are solicitations)
TOTALS	101	4	24	19	6	30	8

posturing in some way to the male are most liable to be molested, either aggressively or sexually. The wing quivering, however, functions as in courtship and reduces the likelihood of a (sexual) attack. Thus the female may usually pass quickly to the nest without the hindrance of the male's provocative solicitations. The male's wing quivering in return reveals the absence of aggression in his welcome. Thus the mutual performance of this posture is of great utility, informing the female that the male will not attack her and the male that she is neither an intruder nor a prospecting female. The strength of the female's tendency to wing quiver or solicit on arrival is indicated by the frequency with which she

performs these patterns even when the male is absent from the territory. In such cases neighbouring males may approach her in attempts at a stolen copulation.

The similarity between these postures and those of late courtship indicates that the same complex of conflicting tendencies is responsible and that the relative dominance of the pair remains unchanged. The persistence of the conflict is due to the continuing sexual potency of the male after his initial courtship and his maintenance of a helmet stage nest in readiness for a fresh mate throughout the whole breeding season. It is thus a feature of the polygamous capacity of the male. It is noteworthy here that the monogamous *Quelea quelea* does not show such intensely sexual greeting behaviour after pair formation, the normal procedure being limited to extensive mutual wing quivering. In other polygamous species [e.g. *P. cucullatus*, *P. (Xanthophilus) aurantius*, and *P. megarhynchus*] solicitation postures are similarly found in both male and female postures in mutual greeting after pair formation. This suggests that where solicitation and pseudo-solicitation are common in courtship they appear also in the greeting behaviour. Thus the relative strengths of the conflicting tendencies (attack, fear, sex) responsible for the postures remain approximately the same both during and after actual pair formation, so long as the male is sexually active in courtship and the pair bond is maintained.

VI. THE BEHAVIOUR OF JUVENILE BIRDS

1. On leaving the nest

Young Bayas are capable of full flight for some twenty to thirty yards on leaving their nest on approximately the fifteenth day (see Ambedkar, in preparation). Frequently during the examination of a nest the young will fly out and flutter off in different directions into the undergrowth. Sometimes, when disturbed, young birds fall into wells and drown. This seems due to a premature departure and does not appear to be a natural occurrence. In spite of attentive watching the natural departure of the young was not observed and very little is known of the role played by the parents at this time. However, one young was seen immediately after its flight from the nest. On the return of the female she fluttered over the young bird and then flew off calling into a near-by stand of sugarcane. The young bird followed it there landing within a few feet of it. The two birds were then lost to view in the dense foliage.

On leaving the colony the young birds scatter and go into dense vegetation. The family does not clump together closely at all and only single juveniles of this age have been seen. One young bird was seen near the Hingane colony shortly after its first flight from the nest and

both parents were seen feeding it. It begged frequently with wing quivering and gave a shrill 'location' call. At greater distances from the colony the young have also been seen sitting still for long periods (up to twenty minutes at least in some cases) and the parents then come and feed them at intervals. The young of one family can generally be located in the same general area although the young are not perched together. One family party was found in dense bushes with a distance of ten to twenty yards separating the three young birds. As the female flies in to feed the young she gives a special *tchrrrrr* which the young birds answer by the 'location' call. As the young become older they begin to flutter more frequently after the parents when they have brought food. They thus begin to show a marked 'following reaction'. One such juvenile was seen pursuing a male as it flew into a tree. The male fed it and flew off about the tree collecting insects. Every few minutes the young would turn toward the parent and flutter towards it landing as if in a supplant attack, exactly on its perch or just beside it. The adult would then usually feed it. In this way the family maintains a loose contact that becomes more effective as the young begin to fly well.

It seems that the young enter flocks when their parents gradually cease responding to their calls. They follow the parents increasingly and gradually mix with other groups. This happens sometime after the 30th day of life. Young birds were seen among adults in flocks, often wing quivering at neighbours, and also among certain other migratory finches (e.g. Blackheaded Bunting, *Emberiza melanocephala*, and Rosefinch, *Carpodacus erythrinus*) common in the Poona area in autumn. When the flock flew off, however, the juveniles often stayed behind not yet showing full social integration with it. Later several juveniles were found together in a group feeding on cereal heads. It is not therefore altogether clear how far the young first form flocks consisting of their own age group alone and how far they integrate directly with adults. Both evidently do occur.

The behaviour of the juveniles on leaving the nest may then be characterised in three stages :

(1) Nest departure and flight from the colony during which the family becomes well scattered.

(2) Sitting still for long periods with little attempt to follow parents.

(3) The following of parents soon develops and leads eventually to the formation of family groups and to joining flocks.

This sequence differs greatly from that followed by juvenile *Quelea* on leaving their nests in Africa. *Quelea* nests are situated in dense thorn bushes and when the young leave them they scramble about the twigs for several days without attempting a single flight. The dense thorns

are a perfect protection and so long as the young birds remain among them they cannot be taken by the various predators that wait beyond it (Morel & Bourlière 1956). While moving about, these youngsters show typical 'contact' behaviour cuddling together and even preening each other (Crook, in press *a*). Both in the *Quelea* and in the Baya the juveniles eventually join flocks in which 'individual distance' is maintained, but the behaviour prior to this differs markedly in the two species. In each case the behaviour seems to provide maximum possible security for the young. Thus for the *Quelea* the thorns are an effective protection and the young keep together. In the Baya scattering and sitting still, in an environment which is itself in no way protective, seems to be safer than any form of social grouping while the birds are incapable of sustained flight.

2. In the first year

In the first monsoon young male Bayas are busy building nests in sites quite separate from those of the adult birds. Nests of juveniles occur in small groups or in isolation but never in the large clusters typical of adult colonies. The young birds do not build very effectively for often their nests are somewhat aberrant in form. At the structures they sing and advertise but the nests are never accepted by females and never finished. Occasionally young males fly into colonies of adults and hop about the nests there in very sleeked nervous postures. They are soon chased out by the adults present. The main burst of building was seen at the onset of the monsoon, but a second outbreak occurred in October when some second broods of adult Bayas were in the nest. Thus juvenile Bayas were busy at fresh green nests in bushes projecting above sugarcane stands at a time when most adults were flocking after leaving their colonies. At this season the male juvenile weavers are a dull grey colour with blackish beaks and can be distinguished from post-breeding adults and from juveniles of the year.

VII. SUMMARY

1. The reproductive behaviour of the Baya Weaver (*Ploceus philippinus*) was studied in the Poona area of western India in the monsoon seasons of 1958 and 1959. The work continues studies by other authors on the species in India and recent comparative work on weaver bird behaviour in West Africa.

2. Of 35 colonies studied 82.8% were situated over water and of these 65.7% occurred either within wells or in trees over them. Only six active colonies were found away from water. The survival value of colony siting is discussed.

3. The tertiary sex ratio as determined in the breeding colonies was 1 male : 1.44 females. This excludes from consideration the non-breeding population of males in their first year of life.

4. Each male builds enough nests for his females and usually maintains an extra 'helmet stage nest' at which he will court any female arriving late in the colony. The numbers of females per territory are shown in Table II. In Table III the numbers of nests per territory and their stages of construction are shown together with the number of females in the territory.

5. The polygamy of the Baya appears to result from the greater availability of females over males in any one breeding season. This is partly due to the failure of males to breed in the first year. Other factors may be important however as the sex ratio of fledgelings is in favour of the males.

6. Males defend small territories around their nest sites. While at first more than one male may build on a nest, mutual hostility soon develops and trespassing is met with aggressive behaviour, the dominant bird at any one site becoming the owner. Occasionally a male may build two nests at once and sometimes these may be in different parts of the colony. In such cases one nest is eventually abandoned and the male's activity concentrated in one place. The size of the territories is influenced by the frequency of suitable nesting sites in a given area.

7. Experimental modification of territories produced the following results :

- a. When occupied nests are moved closer together during brooding an increase in threatening behaviour between neighbouring males occurs.
- b. If the entrance tube of an occupied nest is tilted so that it opens within the territory of a neighbour, the female owner of the nest cannot enter it nor does the male attempt to fight either member of the pair into whose territory the entrance has been moved. The female of the latter pair however enters it without hesitation. The original owner female is driven out when she attempts to reach her own nest entrance.
- c. Unoccupied nests when moved into a neighbouring territory or placed near another male's nest change ownership.
- d. Displacement of nests confuses the females who become very anxious, showing much wing flickering, and visit neighbouring nests. This causes fights between females. Neighbouring males respond to the wanderings of the females with supplanting attacks and occasionally with sexual 'greetings' both of which the females avoid.
- e. If occupied nests are kept with reduced distances between them the aggressive responses of the males gradually fade and

finally the interactions between the members of the two pairs do not differ from those in unchanged territories. The birds thus adapt themselves quickly to a reduced territory size. The defended area can in fact be reduced to little more than the nest itself.

8. Territories are defended by supplanting attacks, lunges, and Tail depressed Threat. Sequences of aggressive behaviour are analysed and the frequencies of different types related to the contexts in which they occur (see Table V). The occurrence of song is discussed.

9. The pairing process of the Baya occurs in two stages : nest invitation by Advertisement Display and pair bond formation during courtship which includes much sexual chasing. The details of the various displays and other behaviour patterns shown are analysed with comparative reference to the behaviour of other colonial Weavers. The observed behaviour is shown to be due to motivational conflicts between tendencies to respond to the female with sex, attack, and escape. The mutual resolution of these conflicts leads to copulation and pair formation. The detailed descriptive data are shown in Schemes A, B, and C which are further analysed and discussed in the text.

10. Following pair formation, behaviour identical with that shown in the final stages of courtship appears in the 'greeting' responses between male and established female whenever they meet in their territory. These may include actual courtship sequences and even copulations. The relative strengths of the conflicting tendencies responsible for the postures remain approximately the same after pair formation so long as the male is sexually active in the courtship of fresh females and the earlier pair bonds are maintained.

11. Juvenile birds scatter on leaving the nest and sit still for long periods during which the parents come and feed them. As their flight improves they begin to follow their parents and gradually form loose family groups. These eventually join flocks of other juveniles or mixed flocks of juveniles and adults.

12. In their first monsoon season juvenile males build nests in sites separated from those of adult birds. The colonies of juveniles are small and often isolated nests built by them are seen. Their nest building is defective and females never accept their nests although they may visit them. First year males in early autumn can be distinguished in the field both from breeding females and the young of the year.

ACKNOWLEDGEMENTS

It is a pleasure to acknowledge the assistance given me by numerous persons throughout the course of these studies. Indeed they would not have been possible without the kindly help I never failed to receive in India,

Dr. Sálím Ali, in particular, has taken a great personal interest in the work at all stages and his detailed knowledge of the species has been a great source of information and renewed initiative. The use of his extensive library whenever required was a kindness I especially appreciated. It was largely due to Dr. Ali that my visit to India became possible and without his help and advice it would have been most difficult to obtain satisfactory results. The success of this endeavour is thus primarily due to him.

Mr. Vijaykumar Ambedkar introduced me to the various colonies around Poona and took part in the investigation at various stages. His assistance in the field on many occasions and his willingness to act as an interpreter helped me greatly at all times. He is at present continuing to work on the breeding biology of the Baya in western India.

On my arrival in Poona Dr. Telford Work, Director of the Virus Research Centre, helped me greatly with certain administrative problems and allowed me to construct aviaries in his garden. Through his assistance I was able to make use of the V.R.C. facilities in numerous practical respects and to benefit greatly, at a later stage, from the help and friendship of his successor Dr. C. Anderson. Dr. Harold Trapido and Dr. Raja Varma also took an interest in the work and were always ready with suggestions and assistance. It was a pleasure to be associated with the work of the V.R.C. on several occasions during my stay.

Mr. John Goatly, regional representative of the British Council in Bombay, gave me much valuable information both before and during my visit to India and did much to help me on several occasions.

I have been in constant correspondence with Dr. W. H. Thorpe, F.R.S., and Dr. Robert Hinde, both of the Zoology Department, Cambridge University. Their continuing advice and encouragement has been of the greatest value. The work is part of a series of Weaver Bird studies financed by the Department of Scientific and Industrial Research, London.

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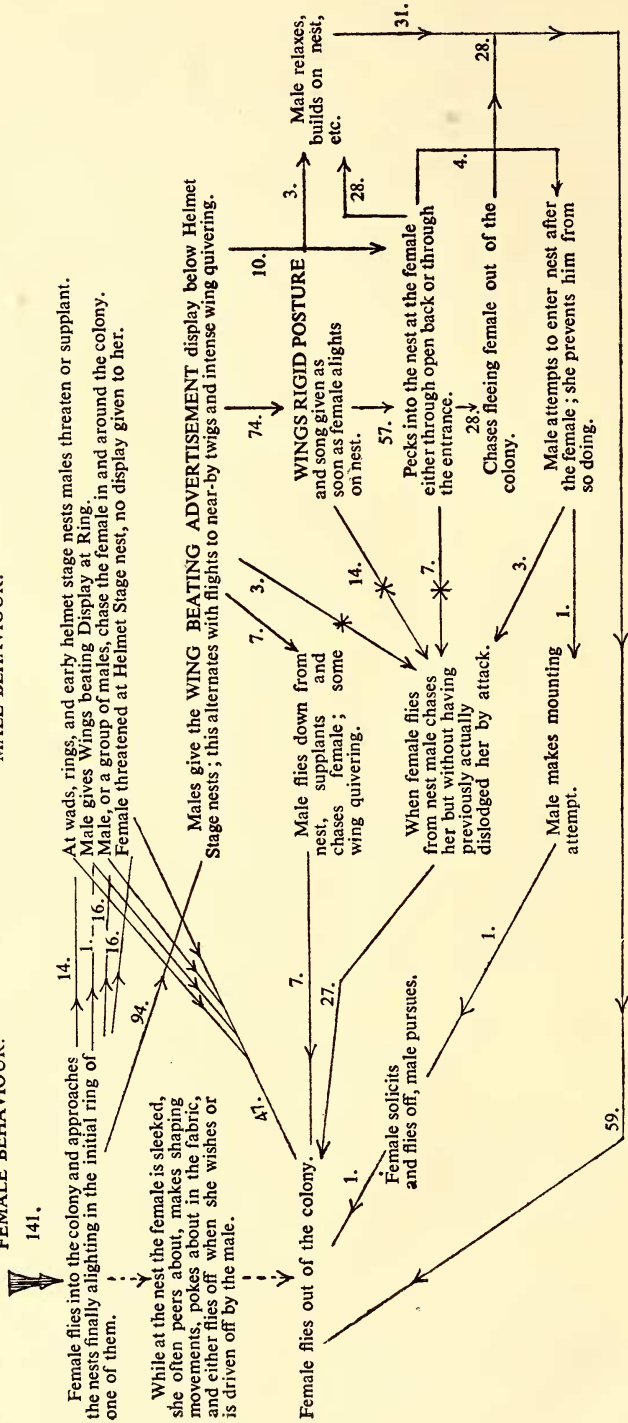
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SCHEME A. BEHAVIOUR SEQUENCES DURING NEST INVITATION

COLONIES IN POONA AREA, JULY-AUGUST 1958

MALE BEHAVIOUR.

FEMALE BEHAVIOUR.

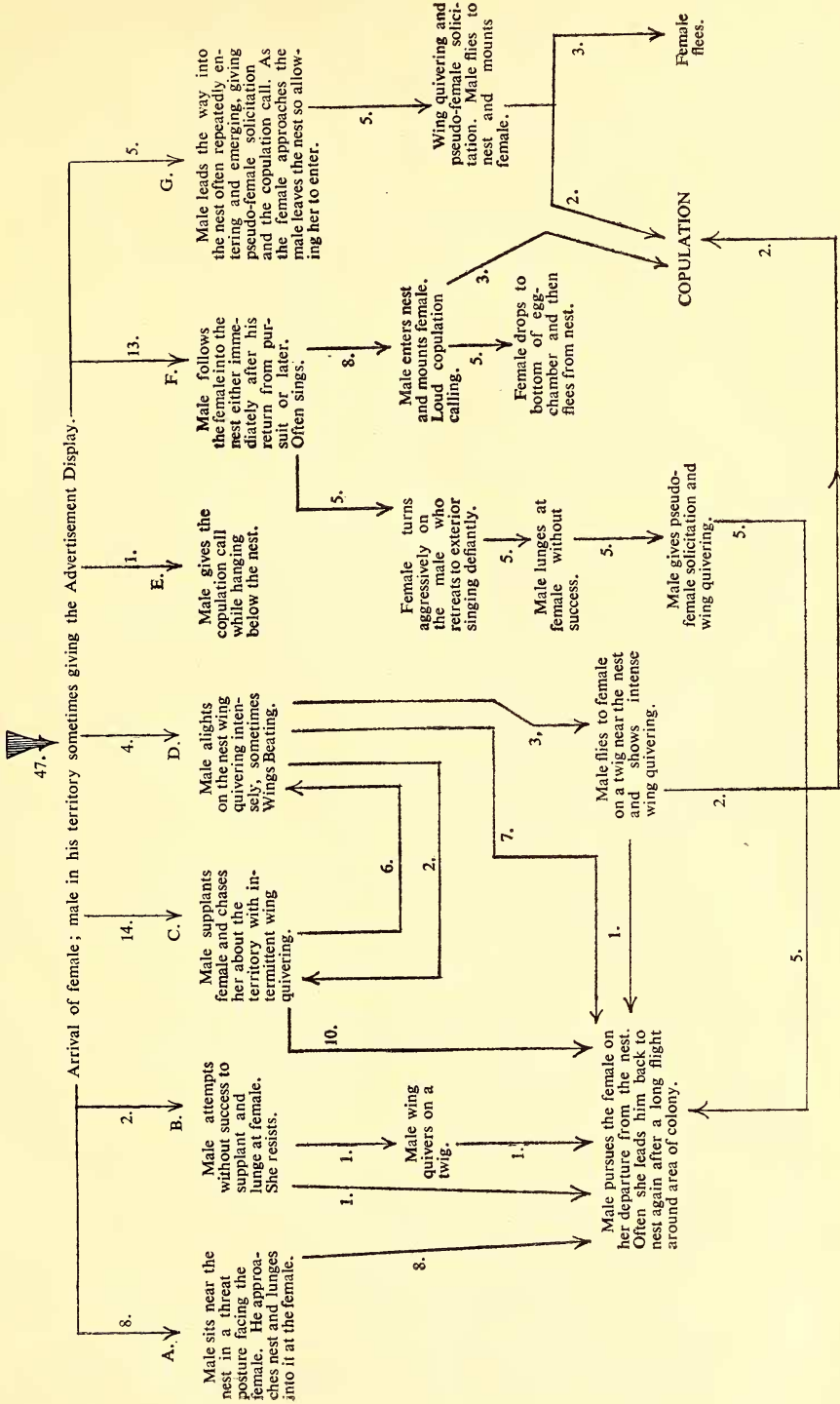


* See Text, p. 24

(NOTE.—The Scheme is read in the following way : 141 sequences of behaviour have been observed. All start with the females' arrival and then pass through various changes, dependent on the males' varying responses, until her eventual departure. Thus following the arrival of a female at a helmet stage nest the male gave the Advertisement display 94 times and this was followed 74 times by the Wings rigid posture. And so on, see further in text.)

SCHEME B. MALE BEHAVIOUR DURING COURTSHIP AND COPULATION FOLLOWING THE ARRIVAL OF A FEMALE IN HIS TERRITORY

HINGANE COLONY, AUGUST 6TH-8TH, 1958



SCHEME C. FEMALE BEHAVIOUR IN COURTSHIP AND COPULATION FOLLOWING HER ARRIVAL IN A TERRITORY
HINGANE COLONY, AUGUST 6TH-8TH, 1958

